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PREDATORS OF THE SWALLOW-TAILED KITE IN SOUTHERN LOUISIANA AND MISSISSIPPI

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ABSTRACT.—We quantified predation on Swallow-tailed Kite (*Elanoides forficatus*) eggs, nestlings, fledglings, and adults on the breeding grounds, Louisiana and Mississippi, U.S.A. Methods included monitoring nests and radio-tagged kites, as well as using Principal Components Analysis to quantify the mobbing intensity of adults toward potential avian predators and other birds that approached nests. We detected 65 predation events while monitoring 317 nesting attempts (1997–2006) and 103 radio-tagged kites (90 fledglings, 13 breeding adults). Predation-related mortality (108–116 depredated kites and eggs) was caused primarily by raptors: 46.0–46.7% by Great Horned Owl (*Bubo virginianus*), 1.7–1.8% by Barred Owl (*Strix varia*), 0.9% by a Red-shouldered or Broad-winged Hawk (*Buteo lineatus*, *B. platypterus*), and 44.9–45.3% by unidentified raptors. Climbing predators were responsible for the remaining predation: 5.1–6.1% by North American rat snakes (*Pantherophis* [= *Elaphe* spp.]) and 0.9% by raccoon (*Procyon lotor*). Kite mobbing behavior during nest defense confirmed the importance of the two owl predators and implicated additional avian predators (e.g., Bald Eagle [*Haliaeetus leucocephalus*] and Red-tailed Hawk [*B. jamaicensis*]) not detected through other methods, although kites sometimes mobbed nonpredators. Altogether, the combined methods indicated that the Great Horned Owl is not only the most frequently documented predator of the Swallow-tailed Kite population under study, but also the only predator known to kill kite adults.

KEY WORDS: *Swallow-tailed Kite*, *Elanoides forficatus*; *Great Horned Owl*; *Bubo virginianus*; *mobbing*; *predation*; *predator identification*.

DEPREDADORES DE *ELANOIDES FORFICATUS* EN EL SUR DE LOUISIANA Y MISSISSIPPI

RESUMEN.—Cuantificamos la depredación sobre huevos, polluelos, volantes y adultos de *Elanoides forficatus* en sus áreas de reproducción en Louisiana y Mississippi, Estados Unidos. Los métodos utilizados incluyeron el monitoreo de nidos y el seguimiento de individuos mediante radio transmisores. Además utilizamos análisis de componentes principales para cuantificar la intensidad del comportamiento de acoso ante depredadores y ante otras aves que se acercan al nido. Detectamos 65 eventos de depredación durante

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el monitoreo de 317 intentos de nidificación (1997–2006) y el seguimiento de 103 individuos marcados con radiotransmisores (90 volantones, 13 adultos reproductivos). La mortalidad causada por depredación (108–116 huevos e individuos depredados) fue en su mayoría causada por aves rapaces: 46.0–46.7% por *Bubo virginianus*, 1.7–1.8% por *Strix varia*, 0.9% por *Buteo lineatus* o *B. platypterus* y 44.9–45.3% por aves rapaces no identificadas. Los depredadores escaladores fueron responsables por la fracción de depredación restante: 5.1–6.1% por *Pantherophis* [= *Elaphe* spp.] y 0.9% por *Procyon lotor*. El comportamiento de acoso ante depredadores durante la defensa del nido confirmó la importancia de las dos especies de búho como depredadores e implicó a otras especies de aves depredadoras (e.g., *Haliaeetus leucocephalus* y *B. jamaicensis*) que no fueron detectadas por otros métodos. Sin embargo, en algunas ocasiones *Elanoides forficatus* también presentó comportamiento antidepredatorio hacia aves no depredadoras. En general, la combinación de métodos no sólo indicó que el búho *Bubo virginianus* es el depredador que se documentó con mayor frecuencia para las poblaciones de *E. forficatus* estudiadas, sino también, que éste es el único depredador de individuos adultos que se conoce.

[Traducción del equipo editorial]

Predation can limit some raptor populations and even structure their communities (Craighead and Craighead 1956, Newton 1979, Petty et al. 2003, Sergio et al. 2003), and valid information on such is often needed for population management and conservation. Predators on nest contents and fledglings have been identified and depredations quantified for some raptor species, e.g., Broad-winged Hawk (*Buteo platypterus*) and Red-shouldered Hawk (*B. lineatus*; Crocoll and Parker 1989, Osprey (*Pandion haliaetus*; Poole 1989), and Prairie Falcon (*Falco mexicanus*; McFadzen and Marzluff 1996), but the predators of many species remain largely unknown.

Choosing methods to quantify predation on raptors and identify predators is challenging because raptor nests and individuals are dispersed widely, and predation events occur infrequently and often at night, reducing the probability of detection. Camera systems arguably provide the most accurate method of surveillance, but risk causing nest desertion (Williams and Wood 2002). Raptors can be sensitive to disturbances during all phases of reproduction, especially during nest-building, egg-laying, incubation, and brooding (Grier and Frye 1987). If cameras are installed after incubation to avoid most disturbance, sampling biases specific to one nest stage or another may result (Williams and Wood 2002).

Predators of the northern Swallow-tailed Kite (*Elanoides forficatus forficatus*), a subspecies of conservation concern, are poorly known (Meyer 1995). Several raptors are potential predators of Swallow-tailed Kite adults, fledglings, and nest contents on the breeding grounds in the southeastern United States, based on range overlap and behavior. The Great Horned Owl (*Bubo virginianus*) predated a variety of raptors from eggs to adults (Bosakowski et al. 1989, Farquhar 1992, Tomazzoni et al.

2004). This species was one of the most important predators on Mississippi Kites (*Ictinia mississippiensis*; Parker 1999) and was also suspected of killing an adult Swallow-tailed Kite (Cely and Sorrow 1990). Barred Owls (*Strix varia*) depredated an adult Snail Kite (*Rostrhamus sociabilis*) and adult American Crows (*Corvus brachyrhynchos*; Sykes et al. 1995, Verbeek and Caffrey 2002). Bald Eagles (*Haliaeetus leucocephalus*) killed adult Osprey and crows (MacDonald 1994, Verbeek and Caffrey 2002), and one was suspected of killing an adult Swallow-tailed Kite (Snyder 1974). Red-tailed Hawks (*Buteo jamaicensis*) depredated adult and nestling raptors, and fledgling and nestling crows (Bent 1937, Peyton 1945, Perkins et al. 1996, McGowan 2001a, Verbeek and Caffrey 2002, Miller 2005). Red-shouldered Hawks depredated crow nestlings (Caffrey 2000) and Swallow-tailed Kite eggs (Short 1974), and a Broad-winged Hawk depredated or scavenged an adult Northern Saw-whet Owl (*Aegolius acadicus*; Rosenfield 1979). Cooper's Hawks (*Accipiter cooperii*) have killed adult and nestling crows (Rosenfield and Bielefeldt 1993, Caffrey 2000). Although cannibalism is probably rare, one adult southern Swallow-tailed Kite (*E. f. yetapa*) was observed removing nestlings from a neighboring nest and feeding them to its young (Vasquez Marroquin et al. 1992).

Other avian predators and scavengers are potential infrequent predators of Swallow-tailed Kite eggs and nestlings. Fish Crows (*C. ossifragus*) and American Crows are confirmed predators and Blue Jays (*Cyanocitta cristata*) suspected predators of raptor nestlings and eggs (Austing 1964, Sykes 1987, Freeman 1993, Parker 1999). Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) depredated nestling wading birds (Bent 1937, Butler 1992), and a Turkey Vulture depredated a nestling Snail Kite (Snyder et al. 1989).

Climbing mammals and snakes are potential predators of Swallow-tailed Kite nest contents and possibly even adults. Raccoons (*Procyon lotor*) depredated raptor eggs and nestlings (Craighead and Craighead 1956, Sykes et al. 1995), and adult Mississippi Kites (Parker 1999), and crow eggs, nestlings, and fledglings (McGowan 2001a, McGowan 2001b). Fox squirrels (*Sciurus niger*) depredated raptor eggs and nestlings (Craighead and Craighead 1956, Parker 1999), and eastern gray squirrels (*S. carolinensis*) depredated crow eggs (McGowan 2001a). Eastern rat snakes (*Pantherophis* [= *Elaphe*] *alleganiensis*) depredated Snail Kite nestlings and eggs (Sykes et al. 1995).

Thus, published reports indicate that a variety of animals probably prey on kites, but little is known of their relative frequency of attack or the risk posed to kites of various ages. In the present study, part of a long-term investigation of Swallow-tailed Kite demography, we combined nest-monitoring and radiotelemetry to identify and quantify predators of the northern Swallow-tailed Kite on its breeding range. We avoided using cameras because the only instance of camera installation during incubation for a Swallow-tailed Kite was followed by nest abandonment (K. Meyer pers. comm.), and because raptors generally may abandon nests if disturbed during incubation (Grier and Frye 1987). We anticipated that we would not be able to deduce the identity of all predators based on evidence left by the predator, nor would our methods allow us to detect all predation events. Thus, to complement these data, we also quantified kites' mobbing behaviors near their nests, a potential way to identify species that kites considered to be a predation risk. This methodology was based on the fact that some species of birds were able to discriminate predator types or species posing different risk levels (McLean and Rhodes 1991).

STUDY AREAS

We studied predation on Swallow-tailed Kites during the breeding season in southern Louisiana and southwestern Mississippi, U.S.A. The two primary study areas were the lower Pearl River-Lake Pontchartrain basins (PPB), Louisiana and Mississippi, and the Atchafalaya River basin (ARB), Louisiana, where we searched for and monitored nests, radio-tagged nestlings and adults, and studied mobbing behaviors at nests (Fig. 1). We searched for radio-tagged kites in these two study areas and also in the Pascagoula River basin, Mississippi (Fig. 1) and occasionally elsewhere (see Methods).

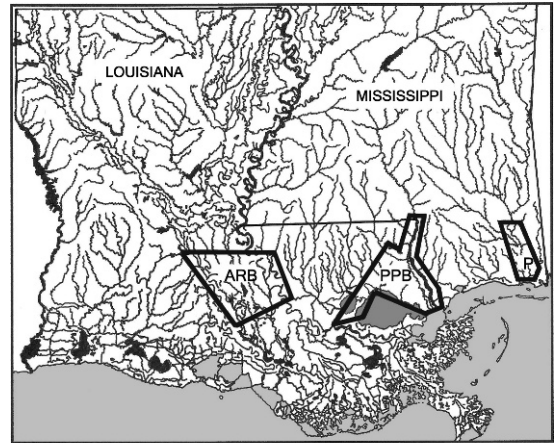


Figure 1. Primary study areas for monitoring of nests and radio-tagged Swallow-tailed Kites, the Atchafalaya River basin (ARB) and lower Pearl River-Lake Pontchartrain basins (PPB). Additional monitoring of radio-tagged kites also occurred in the Pascagoula River basin (P), Louisiana and Mississippi, 1997–2006.

The PPB study area included Pearl River and Hancock counties, Mississippi, and St. Tammany, Tangipahoa, and St. John the Baptist parishes, Louisiana. Of 247 nests, 63.6% were in heavily forested suburban areas, 26.7% were in isolated tracts of forest in rural/agricultural areas, and 9.3% in natural forest. In suburban areas, kites nested primarily in pine forests, the majority dominated by loblolly pine (*Pinus taeda*). In rural/agricultural areas, kites nested primarily in forest tracts dominated by pines (*Pinus* spp.) and secondarily in bottomland hardwood forests, dominated by sweetgum (*Liquidambar styraciflua*). The natural forests kites nested in were almost exclusively bottomland hardwood forests dominated by sweetgum.

The ARB study area, 105 km to the west, included Pointe Coupee, Iberville, St. Martin, and St. Landry parishes, Louisiana. Kites nested in uninhabited bottomland hardwood forests, primarily in stands of eastern cottonwood (*Populus deltoides*) and sweetgum.

The Pascagoula River basin study area is approximately 110 km to the east of the Pearl River basin in Jackson and George counties, Mississippi. Habitat there consists of swamps dominated by bald cypress (*Taxodium distichum*) and black tupelo (*Nyssa sylvatica*).

tica), bottomland hardwood forest dominated by sweetgum and oaks (*Quercus* spp.), and forested bluffs dominated by pines (*Pinus* spp.).

METHODS

Monitoring Nests and Radio-tagged Birds. From 15 March–3 August, 1997–2006, we located Swallow-tailed Kite nests and monitored them at least weekly until they failed or the young fledged. Because some nests, nest trees, and territories used for >1 yr were probably used repeatedly by one or both members of the same pairs, we report “nesting attempts” rather than “nests.” Kites often nested in neighborhoods (defined as a group of 2–5 nests 75–700 m apart; Meyer 1995). If predation occurred in a neighborhood, we increased the frequency of nest checks there to two to seven checks/wk, in order to detect a potentially returning predator. We checked nests from the ground using 10–22 × 50 zoom binoculars or a spotting scope.

Swallow-tailed Kite fledglings often return to the nest to sleep, perch, and feed, making determination of the exact fledging date difficult. Swallow-tailed Kites fledge at about 39 d post-hatching (range = 38–41 d, with nestling day 0 defined as the day the first egg hatched; K. Meyer pers. comm., Meyer 1995). We considered kites 39 d old as fledged (see aging methods below). We monitored nests until they were empty, and we had located at least one fledgling from each successful nest.

From 1997–2006, we radio-tracked kites tagged as nestlings and adults for multiple purposes, including detection of predation events and identification of predators of nest contents, fledglings, and adults. We radio-tagged nestlings age 27–35 d, randomly selecting broods for radio-tagging for the PPB study area from a pool of all nests discovered by and surviving until 15 May. By this date most nests contained nestlings, and the oldest nestlings were <27 d old. We omitted a nest from the pool if it failed before nestlings reached radio-tagging age, if it was inaccessible, if climbing might jeopardize the nest, or if the landowner would not grant access. We also radio-tagged two broods in the ARB study area that we selected because of accessibility. From 1997–2004, we captured breeding adults in open areas near nests using mist nets placed above a tethered Great Horned Owl (Cely and Sorrow 1990). All radiotransmitters (2.5 cm wide × 3.5 cm long, 11.0 grams) had a 2-yr battery life and a mortality sensor (controlled by a motion-sensitive mercury tilt-switch that doubled the pulse rate if the trans-

mitter was motionless for >8 hr; American Wildlife Enterprises, Monticello, FL U.S.A.). We attached transmitters with backpack-mounted Teflon harnesses. The Tulane University Institutional Animal Care and Use Committee approved all protocols for capturing, handling, tethering, and monitoring animals (Assurance Number A3552-01).

We attempted to locate radio-tagged fledglings at least weekly until they migrated or died, using ground and air searches (with an R4000 receiver, Advanced Telemetry Systems, Isanti, MN U.S.A., 172-Cessna fixed-wing aircraft with two four-element Yagi antennas mounted on wing support struts) through 31 August. We also attempted to locate radio-tagged adults and kites surviving to 1 and 2 yr old weekly from 15 March–31 August. We recovered transmitters detected on mortality mode within 0–7 d of discovery.

Search areas and coverage for radio-tagged kites included weekly ground- and air-based searches for the PPB study area from 1997–2006 (Fig. 1). We searched the ARB twice using the airplane in 1997, monthly in 1998, and weekly by ground and air thereafter. Searches of the Pascagoula River basin were all by airplane and restricted to 1–3 times per breeding season from 1997–2004. We also conducted bimonthly searches by air for radio-tagged birds on the following Wildlife Management Areas in Louisiana: Red River, Grassy Lake, and Three Rivers (22 July 2002–31 August 2002, 15 March 2003–31 August 2003, 15 March–20 June 2004), and Attakapas, Maurepas, Joyce, and Manchac (1 July 2003–31 August 2003, 15 March–30 June 2004).

Detecting Predation and Searching for Evidence. While searching for and monitoring kite nests, we opportunistically encountered and recorded locations for the following activity sites of probable predators: raptor and crow nests, raptor roosts, and raptor plucking sites. When we observed evidence that probable predators were nesting (e.g., carrying nest material) we searched the vicinity for ≥30 min. We also noted predation on other large birds. When kites alarm-called, we followed them to try to view a predator. Whenever a nestling or fledgling disappeared, or we detected a transmitter on mortality mode, we conducted a search of the area <150 m from the focal point for evidence. The focal point was the nest, kill site, radiotransmitter’s location, kite roost site, or a raptor’s roost or plucking site.

We recorded the following for each site where we found evidence of predation: type of predation event, numbers and ages of prey, date, time, latitude

and longitude, description of habitat, distance from nest tree, type of evidence, approximate time (hr or d) kite remains had been exposed to elements and decomposers since depredation event, remains of other large birds nearby that might have been killed by the same predator, and mobbing behaviors of adult kites. We asked any nearby human residents if they had observed anything about the kites recently and then asked if they had found a dead kite. We also queried lawn service personnel when they had disturbed evidence to reconstruct the predation event more accurately.

Identifying Predators and Quantifying Predation.

We identified predators by their presence at sites of recent depredation (≤ 5 hr of the event), by finding kite or egg remains in the predator's pellet or dissected stomach, and by inference from multiple lines of evidence at sites where predators killed and/or consumed prey. We tabulated the number of eggs or kites depredated by age-category: eggs, nestlings, fledglings, 1- and 2-yr olds, and breeding adults, combining predation detected by nest monitoring and radio-tracking. We did not measure clutch size at nests to avoid causing abandonment. However, one clutch size was determined by killing and dissecting the predator (a midland rat snake, *P. [= E.] spiloides*). For all other nests we estimated a mean clutch size of 2.11 eggs calculated from 151 museum clutches (southeastern U.S.) and measurements at 11 Florida nests (Meyer 1995). We determined brood size from ground observations, 0.5–2 wk post-hatch, using spotting scopes until at least three feedings occurred, and for a minimum of 2–5 hr, depending on nest visibility. For eight nests that failed before brood size was determined, we used a range of 1–2 nestlings killed, because broods of 3 are rare (1.3% of 156 Florida nests; Meyer 1995). We also determined the number of kites killed by examining feathers (number, stage of development, sequence of primaries, secondaries, and rectrices), bones, and other remains.

We used several methods to determine ages of kites or eggs at the time of mortality. For nest contents, if the onset of incubation was known, we used forward dating. We standardized the incubation period to 31 d (beginning on day 0 = date pair began sitting continuously, with hatching of the first egg on day 31), based on a mean incubation time of 31.5 d for six nests reported by Gerhardt et al. (1991) and the artificial incubation of 3 eggs with a minimum possible mean incubation time of 30.2 d (J. Coulson and T. Coulson unpubl. data). If incubation started

between nest visits, we used the midpoint as the onset. We also observed young nestlings (≤ 15 d old) through a spotting scope and compared size and feather development to reference photographs of captive-reared known-aged nestlings ($N = 4$; J. Coulson unpubl. data). We also compared growth measurements (wing chord, tarsus) and feather development from banded nestlings and from remains of depredated young to reference photographs and growth measurements of the known-aged kites.

We defined a predation "event" as an attack occurring on 1 d; multiple attacks on young from the same nest, constituting multiple events, occurred only five times. Nest depredation events often involved >1 death, in the case of eggs and nestlings ($N = 32$ – 34), but also occasional cases of an adult and eggs/nestlings ($N = 18$).

Observations of Potential Predators. We hypothesized that the intensity of kite nest defense behaviors would reflect the risk level posed by the potential avian predator. Based on reports from the literature, we predicted that the most dangerous potential predators of kites, those capable of depredating adults (Great Horned Owls, Red-tailed Hawks, Bald Eagles, and Barred Owls), would be mobbed most fiercely. Adults would respond with an intermediate level of mobbing intensity toward smaller potential predators capable of depredating nestlings and possibly occasionally fledglings (Red-shouldered Hawks, Broad-winged Hawks, and Cooper's Hawks). Finally, adults would respond to potential predators of eggs and small nestlings (American and Fish crows, Blue Jays) with the lowest level of mobbing intensity.

From 1996–2004, we recorded the level of mobbing response (if any) by adult kites to potential avian predators and other species of birds that came within 100 m of a nest. Our sampling scheme was opportunistic within the following framework. We sampled 5–20 nests/yr from 41 neighborhoods. We observed nests for 1–8 hr sessions, sampling throughout the nesting cycle with multiple sessions at some nests. When a potential avian predator or other bird approached a nest we recorded date, nest identity, species of intruder, and seven response variables: (1) duration of event (categorized into five classes, in min: 0, >0 – <2.5 , 2.5 – <5 , 5 – <30 , 30 – 60), (2) number of kites responding, (3) number of kites alarm-calling, (4) number of kites circling over intruder, and number of times responding kite(s) used each of several behaviors: (5) chase, (6) swoop over, or (7) strike predator. Mobbing responses included multi-

ple observations for the same and/or different species of birds at some nests. We excluded responses of nesting Swallow-tailed Kites to conspecifics.

Analyses of Mobbing Response and Predation Risk. We used two approaches to assess our general hypothesis about a positive relationship between risk level and mobbing response intensity. First, we calculated the frequency with which adults did not respond to potential avian predators and other birds that approached nests. We predicted that kites would respond along a tolerance gradient whereby adults would exhibit no response toward those species posing little or no risk of predation to themselves and their offspring and would always mob potential predators of adults. We used all observations, including repeated sampling sessions at some nests and also multiple responses recorded at individual nests for the same and or different potential avian predators.

Our second approach involved a subset of the data used in the first approach and the seven mobbing response variables. We expected most or all variables to be correlated, because all involved some measure of the intensity of the mobbing response (Newton 1979, Fox and Donald 1980, Wiklund and Village 1992, Arroyo et al. 2001). We used Principal Components Analysis (PCA) with Varimax rotation as a descriptive tool to quantify these potentially correlated responses. PCA was also used to assess whether these seven variables represented one or more fundamental variables (which would be revealed by multiple significant Principal Components), to differentiate between behavioral responses directly related to predation risk and those that were not, and to identify patterns of variation in mobbing responses toward different potential predators.

Prior to conducting the PCA, we reduced the data to a set of independent data points by using mobbing behaviors toward only one potential predator species for each nest. If we observed kites at a particular nest responding to more than one species, we randomly selected one species for inclusion in the PCA. If we had multiple observations for this species at a nest, we used the mean of the responses for each variable.

RESULTS

We monitored 317 nesting attempts, averaging 1.2 visits/wk over 2290 nest-wk. We radio-tagged and monitored 93 nestlings, 90 of which fledged, and 13 breeding adults. We also monitored radio-tagged kites surviving to 1 yr ($N = 41$) and 2 yr of

age ($N = 28$). We detected 65 predation events which resulted in the death of 108.3–116.3 kites and eggs (range indicates uncertainty as to number of nestlings involved; fractions of kites/eggs depredated occurred because we used a mean clutch size of 2.11 eggs when clutch size was unknown). We observed mobbing responses or no response for adult kites at 131 nesting attempts during 260 sessions in which potential avian predators and other birds approached nests.

Predation of Nests and Fledglings. Predators left diverse kinds of evidence (Table 1). One piece of evidence was sometimes enough to identify the predator (e.g., kite remains in a Barred Owl's pellet), but we typically used multiple lines of evidence to deduce the predator's identity (e.g., plucked, partially eaten carcasses on nest and adult kites vigorously mobbing a Great Horned Owl in nest tree 48 min after sunrise, Table 1).

Most deaths from predation (93.9–94.4%) were caused by raptors, with the remainder by climbing mammals and snakes (Table 2). The Great Horned Owl was responsible for the greatest amount of predation overall, on the following age groups: eggs, nestlings, fledglings, and breeding adults (46.0–46.7%; Table 2). This was the only species we documented preying on adults. We also documented the following species as predators on kites: Barred Owl (nestlings), a Buteo (either a Red-shouldered or Broad-winged Hawk; nestling), western and midland rat snakes (*P. [= E.] obsoleta* and *P. [= E.] spiloides*; eggs and small nestlings), and raccoon (nestling).

Mobbing by Kites. Kites mobbed individuals of 16 avian species that approached nests (Fig. 2). Kites showed no or variable response to certain species and always responded to others (Fig. 2). The most tolerance was shown toward Mississippi Kites and corvids, which were often ignored. In contrast, kites always responded aggressively toward large owls, Bald Eagles, Red-tailed Hawks, Cooper's Hawks, and large herons.

PCA revealed only one principal component with an eigenvalue >1 (3.845). This Principal Component-I (PC-I) explained 54.9% of the total variance. Loadings of variables on PC-I were as follows: *number of kites responding*, 0.924; *alarm-call given*, 0.844; *duration of response*, 0.832; *circle over*, 0.790; *swoop over*, 0.663; *chase*, 0.656; *strike*, 0.301.

Because the loading of the variable *strike* was weak (Comrey and Lee 1992), we conducted a second PCA including all the same variables except *strike*, and PC-I then explained 62.9% of the total variance

Table 1. Types of evidence used to detect predation and identify predators on Swallow-tailed Kites.

Predation occurred at night.

Predation occurred on nest.

Predator plucked feathers from kite.

Predator ripped off and discarded wing, usually by breaking humerus into pieces.

Predator decapitated kite by breaking the neck, discarding head.

Predator discarded the meaty part of tail with feathers attached.

Predator twisted a long bone causing a spiral, compound fracture.

Predator ripped off and discarded a leg.

Tooth impressions from a carnivorous mammal on feathers and or bones.

Some bones and/or fragments picked clean by predator, no chew marks; ribs sometimes broken and twisted, but pieces of rib often remaining attached.

Predator ate >400 g of prey in one feeding; determined only at sites where depredation occurred ≤ 5 hr prior to discovery.

Kite's body is size of adult or nearly so (applied to kites ≥ 27 d old), making predation by an intermediate-sized raptor less likely.

Predator fed on kite carcass over a 2-d period.

Predator flew with a grown kite's carcass, carrying it away from kill site.

Mammalian predator dragged kite remains along its trail; feathers entangled in ground cover.

Clutch of kite eggs found in stomach of rat snake.

Kite remains and/or pellet(s) containing kite remains and/or transmitter under Great Horned or Barred Owl day roost and/or plucking site.

Recently regurgitated pellet from a mid-sized hawk at kill site containing only nestling kite feathers (no bones), from either a Broad-winged or Red-shouldered hawk.

Fresh predator excreta next to hawk pellet from a Broad-winged or Red-shouldered hawk.

Freshly molted Great Horned or Barred Owl feather amidst kite remains.

Freshly shed skin from a rat snake on trunk of nest tree or beneath nest when nest contents disappeared.

Fresh raccoon feces near kite remains.

Spider or caterpillar webs covering underside of nest or trunk, immediately below nest undisturbed, indicating non-mammalian predator.

Parents and neighborhood members circled over kill site and/or predator while alarm calling.

Kite colony observed mobbing Great Horned Owl ≤ 5 hr of predation event.

Sibling killed by a Great Horned Owl.

Sibling killed by unidentified species of raptor.

Great Horned Owl depredated nearby kite nest(s).

Unidentified species of raptor depredated nearby kite nest(s).

Great Horned Owl observed or heard calling near active kite nest.

Bald Eagle and Red-tailed Hawk not present in neighborhood when predation occurred.

(eigenvalue = 3.776). We interpreted this PC-I as a measure of mobbing intensity (Fig. 2; species shown by increasing rank on PC-I) because loadings of all response variables were strongly positive with respect to this axis. The new loadings of original variables on PC-I in this second analysis were as follows: *number of kites responding*, 0.928; *alarm-call given*, 0.848; *duration of response*, 0.827; *circle over*, 0.804; *swoop over*, 0.663; *chase*, 0.653.

Mobbing intensity (PC-I) was greatest toward Great Horned Owls, followed by other large nocturnal (Barred Owl) and diurnal (Red-tailed Hawk, Bald Eagle) raptors (Fig. 2). Mobbing intensity was of an intermediate level when directed toward mid-sized diurnal raptors (Red-shouldered Hawk, Broad-

winged Hawk, Cooper's Hawk), a large raptor that is a fish-specialist (Osprey), and large herons. Mobbing intensity was lowest toward vultures, corvids, and Mississippi Kites. *Strike* frequency, retained as a separate variable, tended to increase in parallel with PC-I scores starting with the species with the lowest PC-I scores, but then decreased in importance for the three most intensively mobbed species: Red-tailed Hawk, Barred Owl, and Great Horned Owl (Fig. 2).

Other responses of adults to potential predators were rare. When a Blue Jay alighted on a limb below a kite nest, one kite walked stiffly across the limb toward the jay with beak open and wings almost fully extended, while its incubating mate alarm-called. At another nest, a brooding kite positioned itself be-

Table 2. Contributions by each predator to age-specific Swallow-tailed Kite predation affecting 60 nesting pairs and/or their young/eggs, 1997–2006.

AGES OF KITES OR EGGS	PREDATORS									
	TOTAL					SUSPECT				
	KILLED OR DESTROYED	GREAT HORNED OWL	GREAT HORNED OWL ¹	LARGE RAP. TOR ²	BARRED OWL	RSHA OR BWHA ³	UNKNOWN RAPTOR ⁴	RAT SNAKE	RACCOON	
Eggs	27.3	10.5	8.4	4.2						4.1
Nestlings	47–55	20–23	5	11–14	2	1	6–7	1–2		1
Fledglings	16	10	2	4						
Adults	18	10	3	5						
Total predation mortality	108.3–116.3	50.5–53.5	18.4	24.2–27.2	2	1	6–7	4.7–5.3		1
Predation (%) due to predator		46–46.7	15.9–17.0	22.4–23.4	1.7–1.8	0.9	5.5–6	5.1–6.1		0.9

¹ Suspect Great Horned Owl = suspect Great Horned Owl was predator due to circumstantial evidence; predator is a large raptor.

² Large Raptor = predator definitely a large raptor of the following possibilities: Great Horned Owl, Red-tailed Hawk, Bald Eagle, or Barred Owl(?).

³ BWHA or RSHA = predator was either a Red-shouldered or a Broad-winged hawk.

⁴ Unknown Raptor = predator definitely a species of raptor, medium to large, of the following possibilities: Great Horned Owl, Barred Owl, Red-tailed Hawk, Bald Eagle, Red-shouldered Hawk, Broad-winged Hawk, or Cooper's Hawk.

tween its 7- and 10-d-old nestlings and two Blue Jays that alighted in the nest tree. The kite shifted its position on the nest three times according to where the jays moved in the tree.

Methods of Detecting Predation and Identifying Predators. We detected 83.1% ($N = 65$) of predation events because of nest-monitoring and 16.9% via radiotelemetry. We identified to species 55.6% of 54 predators detected during nest-monitoring and 63.6% of 11 predators during radio-tracking. Of 17 depredation events involving nestlings old enough to be radio-tagged (≥ 27 d), 11.8% were detected by radio-tracking. We detected 56.2% ($N = 16$) of depredation events involving fledglings by radio-tracking. We did not detect any predation on radio-tagged 1- or 2-yr-old or adult kites. We detected all predation on adults ($N = 18$) by frequent monitoring of nests.

DISCUSSION

Predators of Kites. Our results indicated that other raptors were the primary predators of Swallow-tailed Kites and their nest contents in southern Louisiana and southwestern Mississippi during the breeding season (Table 2). Avian predators not identified to species were the main nest predators in Florida (Meyer and Collopy 1990) and also Guatemala, along with monkeys (Gerhardt et al. 1991). Large raptors and mammals were the primary nest predators for the ecologically similar Mississippi Kite on the Great Plains (Parker 1999).

Raptors probably accounted for a large proportion of the predation on kites in our study for several reasons. One possible explanation is the abundance and diversity of raptors present in the subtropical ecosystems where the kites nest. Also, kites effectively defended their nests against some of the other potential avian predators in the region. We were unable to explain the low incidence of predation by climbing mammals.

The Great Horned Owl was the primary predator on all ages of Swallow-tailed Kites in our study areas. This species accounted for at least 46.0–46.7% of documented predation and was likely responsible for >61.9–63.7% (Table 2). Great Horned Owls were also main predators of Mississippi Kite adults and nest contents on the Great Plains, sometimes depredating entire colonies (Parker 1999).

Our methods may not have detected all predation or predator species. We probably underestimated depredation of eggs and nestlings because we could not ascribe a cause of failure for 22.5% of failed

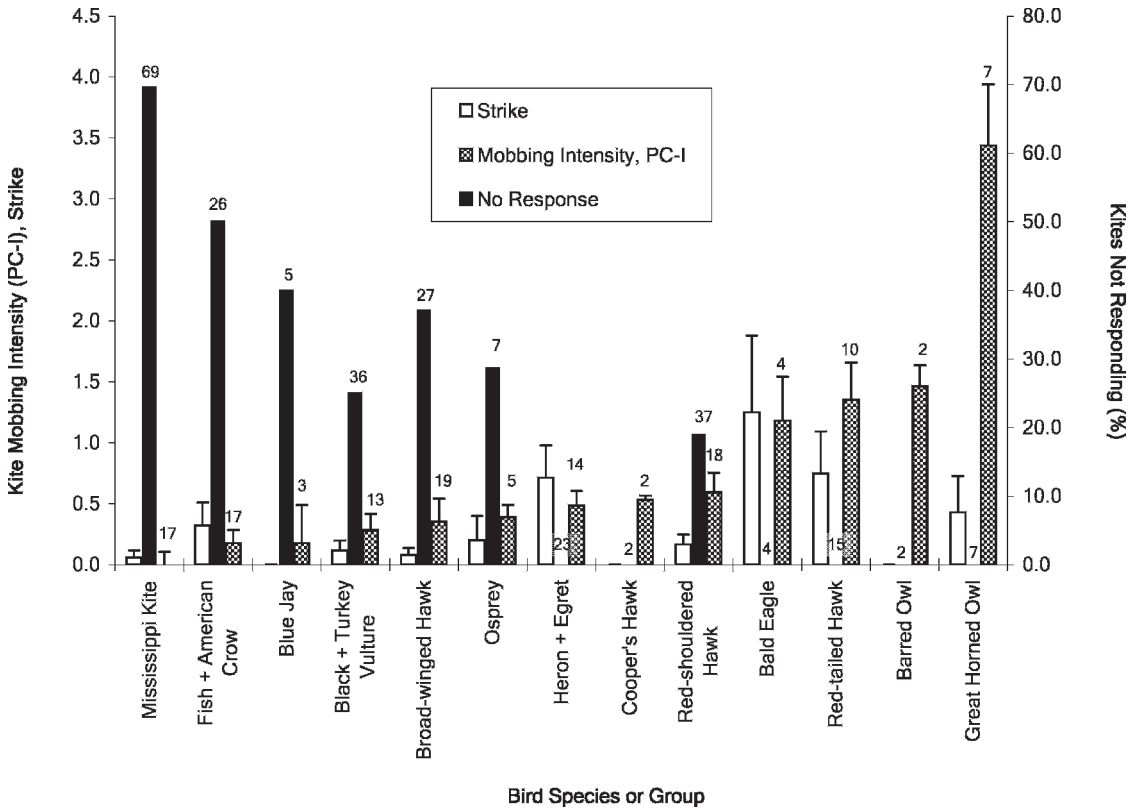


Figure 2. Swallow-tailed Kite responses, or lack thereof, to 16 species combined into 13 groups (Heron + Egret = Great Blue Heron plus Great Egret [*Ardea alba*]) of potential predators and other birds near nests, 1996–2004. Thirteen groups ranked, left to right, by increasing intensity of overall mobbing intensity. Y-axis 1: The mobbing intensity of Swallow-tailed Kite toward potential avian predators and other birds near nests, as measured by our principal components analysis, first principal component (PC-1) and the frequency of kites striking potential predators (*strike*); *N* = number of observations per predator species or group and number of nests for which observations occurred; error bars represent SE. Sample sizes are above bars; *N* is identical for mobbing intensity (PC-I) and *strike*. Y-axis 2: Swallow-tailed Kites not responding to potential predators (% of all observations for each species); *N* includes multiple observations for some nests. Sample sizes for zero values are above the X-axis.

nests (*N* = 27 of 120). We suspect that rat snakes caused some of these failures because this predator often left no evidence, and most of the nests for which we could not assign a cause of failure failed in the egg or small-nestling stage. We probably also underestimated predation of fledglings, including radio-tagged ones, because some whose signal we no longer detected may have been taken by a predator. Although we reported age-specific depredation, some predators probably depredate additional ages of kites. Rat snakes may be capable of killing large nestlings and adults (see Williams 1951). Raccoons have killed incubating adult Mississippi Kites (Parker 1999) and might also kill adult Swallow-tailed Kites.

Both frequent monitoring of nests and radiotelemetry contributed valuable information about predators and their frequency of predation. Frequent monitoring detected most nest depredation in our study. However, 14% of 28 nest predators identified to species were identified through use of telemetry.

Predators of Raptors and Effects of Predation. Although raptors generally experience lower predation rates than other birds (Ricklefs 1969, Newton 1979), predation can affect raptor populations and communities. Predation on other raptors and their nests by large, dominant owls, particularly Great Horned Owls and Eurasian Eagle-Owls (*Bubo bubo*), is well documented (Mikkola 1976, Newton 1979, Mikkola 1983). In many cases *Bubo* owl predation

on other raptors does not affect prey populations, but an increasing number of studies report measurable negative effects on raptor density, abundance, productivity, and nesting distribution, or an increase in the number of immature females as breeders (Craighead and Craighead 1956, Cugnasse et al. 2003, Sergio et al. 2003, Sergio et al. 2005, Kenward 2006, Coulson 2006).

Predation risk has been related to proximity of the raptor's nest to the predator's territory. Sergio et al. (2003) used distances from Black Kite (*Milvus migrans*) nests to those of their primary predator, the Eurasian Eagle-Owl, as estimates of predation risk. Black Kite mean productivity was explained by the interaction of predation risk and food abundance, and pairs nesting ≤ 1 km from an owl nest did not fledge young. We found that some Swallow-tailed Kite neighborhoods were more prone to Great Horned Owl predation than others: in high risk neighborhoods, owls depredated multiple incubating/brooding adults and/or nest contents within and among years. Predation risk may have been related to the proximity of kite nests to owl territories and/or predation habits of individual owls.

Mobbing Intensity and Predation Risk. Our mobbing study results suggest that a complex array of factors probably determines the Swallow-tailed Kite's intensity of mobbing response toward potential predators. Our original hypothesis, that mobbing intensity was positively related to predation risk, was supported by our principal components analysis (PC-I, interpreted as mobbing intensity, Fig. 2). The frequency with which kites failed to respond to predators also supported this hypothesis, in that adults always responded to three potential predators of adult kites, but exhibited more tolerance toward egg and nestling predators (Fig. 2). However, examination of the rate at which adults struck potential predators, the most aggressive mobbing response observed, suggested an alternative hypothesis: adults strike nest predators that pose less direct risk to themselves more aggressively than those that constitute a higher potential risk to adults. This might explain why adult Swallow-tailed Kites did not strike Great Horned Owls more often than other potential predators (Fig. 2). Perhaps adult kites risk being captured or injured when striking this owl and other large predators such as Barred Owls and Red-tailed Hawks (McLean and Rhodes 1991).

Other factors such as instinct, competition, and nest stage may also influence mobbing response and intensity. Swallow-tailed Kites may have mobbed

nonpredators (e.g., Osprey, Great Blue Heron [*Ardea herodias*]) because they are innately predisposed to attack any large raptor or bird that flies near their nest (Lorenz 1939). Meyer (1995) suggested that some of the aggression Swallow-tailed Kites showed toward Red-shouldered Hawks was based on food competition. Perhaps Swallow-tailed Kites mob Mississippi Kites because they compete for food, territories, or other resources. The number of kites mobbing is probably partly related to neighborhood size, as has been demonstrated experimentally for a colonial nesting raptor (Montagu's Harrier [*Circus pygargus*]; Arroyo et al. 2001). In raptors such as the Red-tailed Hawk and Eurasian Hobby (*Falco subbuteo*), the intensity of nest defense toward humans was positively related to increasing age of nest contents (Andersen 1990, Sergio and Bogliani 2001), corresponding to increased parental investment (Montgomerie and Weatherhead 1988). We did not address nest age, and this potential source of variability may have affected our interpretation of mobbing intensity data.

Results of our principal components analysis (PC-I, mobbing intensity) underscored our conclusion that the Great Horned Owl and other raptors were the primary predators on adult kites, fledglings, and nest contents. Like Swallow-tailed Kites, Mississippi Kites also mobbed the Great Horned Owl with the greatest intensity (Parker 1988). Swallow-tailed Kite mobbing responses to Great Horned Owls and other large raptors tended to be longer in duration and to include more responding kites than responses to other predators. Harriers respond in greater numbers to decoys of predators of adults than to those posing little or no risk to adults (Arroyo et al. 2001). Considering other potential avian predators, the results of our principal components analysis suggested that our study may have underestimated the importance of the Barred Owl and failed to identify as actual predators species of large diurnal raptors such as Red-tailed Hawk and Bald Eagle, and possibly other avian predators.

Conclusion. In our study areas, raptors, especially the larger species, were the most frequent predators of northern Swallow-tailed Kites on their breeding grounds. Great Horned Owls accounted for the majority of all predation, and this species was the primary predator of Swallow-tailed Kites of all ages. Results from the mobbing-intensity study supported predation-related mortality results obtained from the nest- and fledgling-monitoring study by independently confirming several aspects of Swallow-

tailed Kite predation. Kite mobbing behaviors suggested the following: (1) raptors posed more risk to nesting kites than did other avian predators, (2) larger raptors posed more predation risk than smaller ones, and (3) large owls, particularly the Great Horned Owl, posed the greatest risk.

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